

Embryonic and larval development of big-scale sand smelt *Atherina boyeri* (Atherinidae)

by

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ABSTRACT. - The embryonic and early larval development of the laboratory-reared big-scale sand smelt, *Atherina boyeri* Risso, 1810 are described. Mature unfertilized eggs were pelagic and spherical with a homogeneous and unsegmented yolk containing several oil droplets. Eggs were equipped with long filaments. Fertilized eggs ranged in diameter from 1.58 to 2.05 mm, with a mean ($\pm$ SD) of 1.75 ± 0.10 mm. Embryonic development lasted 211 h 32 min at a mean temperature 19.2°C. Newly hatched yolk-sac larvae measured 4.5 ± 0.15 mm total length. The yolk was completely absorbed by day 3 after hatching. Changes in length and shape of yolk-sac larvae and larvae during the first six days after hatching are also presented.

RÉSUMÉ. - Développement embryonnaire et larvaire d'*Atherina boyeri* (Atherinidae).

Le développement embryonnaire et larvaire précoce de l'athérine *Atherina boyeri* Risso, 1810, élevée en laboratoire, est décrit. Les œufs fertilisés étaient pélagiques et sphériques, avec un jaune homogène et non-segmenté, contenant de nombreuses gouttelettes d'huile. Les œufs portaient de longs appendices filamenteux. Les œufs fertilisés avaient un diamètre de 1,58 à 2,05 mm, avec une moyenne ($\pm$ SD) de $1,75 \pm 0,10$ mm. Le développement embryonnaire a duré 211 h 32 min à une température moyenne de 19,2°C. Les larves nouvellement écloses mesuraient de $4,5 \pm 0,15$ mm de longueur totale. Le vitellus était complètement absorbé trois jours après l'éclosion. Des changements de longueur et de forme des larves pendant les six premiers jours après l'éclosion sont également présentés.

Key words. - Atherinidae - *Atherina boyeri* - Embryo - Larvae - Development.

Atherina boyeri Risso, 1810 is a small, schooling, euryphagous mainly zooplanktophagous (Bartulović *et al.*, 2004a), highly euryhaline (from hypersaline water to fresh-water) atherinid, commonly found in coastal waters of the Mediterranean and the Atlantic, from Madeira to Portugal (Jardas, 1996). Localized populations of *A. boyeri* have been recorded from northern Europe and the British Isles, especially from areas of thermal enrichment (Palmer and Culley, 1983). *A. boyeri* is frequently found in river estuaries (Bartulović *et al.*, 2004b; 2006); however, isolated populations inhabiting entirely freshwaters systems are known to exist in the Mediterranean basin (Tortonese, 1975).

Information on early development stages of *A. boyeri* is sparse and rather confused. Descriptions of eggs were presented by Palmer and Culley (1983) and Creech (1992). To our knowledge, the descriptions of *A. boyeri* larvae have been provided by Vialli (1937: Pl. 34, figs. 4-8) (illustrations are provided by Holt, 1899: Pl. 9, figs. 95-96, and refer to metamorphosed individuals). Information is also available on larvae development in a landlocked population in Lake Trichonis (Greece) (Daoulas *et al.*, 1997). Some data are available on the morphological development of two atherinid taxa that inhabit the European Atlantic coasts (*A. presby-*

ter Linnaeus, 1758) and the Black Sea (*A. mochon pontica* Eichwald, 1838). However, the systematic status of these taxa is still quite uncertain; sometimes they are considered as phenotypic variants of *A. boyeri* (e.g. Bamber and Henderson, 1985) but most often are given a separate specific status.

This paper presents data on the embryonic and larval development in aquaria conditions at ambient temperature and descriptions of early life history stages of *A. boyeri*.

MATERIAL AND METHODS

Mature adults of *A. boyeri* were obtained by micro-mesh beach seine from the Kaštela Bay (middle Adriatic). Males were ranged between 3.4 and 6.7 cm in total length (TL), while females between 5.0 and 8.1 cm TL. Specimens were transferred alive to the laboratory and placed in a 250-l tank with the addition of pure oxygen. The milt was taken from the males using sterilized syringes, taking particular care to maintain the anal area dry, to prevent contact of urine and other metabolic products with the milt. The syringes were then placed on ice and refrigerated. The females were dried

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well with a paper towel, and the eggs striped out in a clean and dry bowl. The milt was then spread over the eggs and all was carefully mixed. The fertilized eggs were transferred to several 150-l incubators at ambient salinity, temperature and natural photoperiod. A temperature ranged between 18.2 and 19.9°C (mean $19.16 \pm 0.42^\circ\text{C}$), salinity 37.6 and 38.2 psu (mean 37.95 ± 0.159 ppt), oxygen 7.8 and 8.3 mg.l⁻¹.

Embryonic development was observed under a binocular microscope. The diameters of the eggs were measured. Early ripening eggs, centred on the largest mode, were yellow in

colour and ranged in diameter from 0.84 to 1.25 mm. The remainder of the eggs consisted of white opaque recruitment eggs (0.08 to 0.42 mm in diameter) and orange opaque late ripening eggs (0.42 to 0.84 mm in diameter). One hour after fertilization, a sample of 10-15 eggs was taken every 7-10 min to determine the exact time of first cleavage. Embryogenesis was examined at different time intervals. Anaesthetized larvae in live condition were measured to an accuracy of 0.01 mm using an ocular micrometer attached to a binocular microscope. The following measurements were taken:

Table I. - Embryonic development of *Atherina boyeri* at mean temperature 19.2°C. [Développement embryonnaire de *A. boyeri* à la température moyenne de 19,2°C.]

Time	Stage	Description
0:00	Fertilization	
1:15	2 cells	Meridional first cleavage
2:23	4 cells	Second cleavage
2:56	16 cells	Cleavage parallel to the second
3:26	32	Cleavage parallel to the first
5:50	Morula	Mulberry stage
7:48	Blastula	Visible blastocel, oil bead is concentrate, germinative ring
8:50	Gastrula	Gastrulation starts
9:06	Gastrula	Yolk being englobed by the blastodisc
17:57	Gastrula	Invagination of blastomeres ends
23:55	Neurula	Formation of neural groove starts
25:33	Neurula	Formation of embryo begins, notochord
27:11	Embryo	Optic vesicles and forebrain formation in begins
27:45		Somatic segmentation is started
28:30		Optic vesicle formed
29:40		Olfactory lobes differentiation, melanophores appear along dorsal side
31:50		Somites and melanophores on the body clearly visible
33:13		Optic vesicle and olfactory lobules clearly visible, somite differentiation completed
37:32		The embryo occupies half the circumference of the egg
40:34		Cardiac contractions (38 min ⁻¹), blood circulatory system is visible on the yolk-sac
45:14		Head is close to oil drops
50:23		Cardiac contractions (64 min ⁻¹)
53:10		Tail lifted of the yolk-sac
55:29		Tail movement begins every 2 min
60:55		Eyes pigmentation is completed, cardiac contractions (105 min ⁻¹)
65:07		Tail movements every 20 s
69:20		Formation of jaw begins
74:47		Melanophores are visible on the yolk-sac, tail tip almost touches the head
80:22		Tail tip almost touches the head
89:33		Cardiac contractions (117 min ⁻¹), Embryo with yolk-sac turning around axis in egg
103:46		Pectoral fin is visible
113:21		Tail (overgrown) is behind head, progressive development of interior organs
130:43		Pectoral fin start move
141:06		Blood is red colour
152:28		Tail is far behind head with movements every 20 s
164:54		Jaw formation is completed
171:12		Mouth is open
189:54		Cardiac contractions (125 min ⁻¹),
211:32	Free yolk-sac larvae	Hatching begins
213:54		All eggs hatched

total length, the distance along the midline of the body from the tip of the snout to the end of the caudal fin; notochord length, the distance along the midline from the tip of the snout to the end of the notochord; head length, the distance between the tip of the upper jaw and the cleithrum; preanal length, distance along the midline of the body from the tip of the snout to the vent; body depth, the perpendicular depth of the trunk at the anus; greatest body depth, body depth at its widest point; yolk-sac volume and horizontal eye diameter. The mouth width of larvae was also recorded. About 10-15 living larvae were used for each measurement.

The time of yolk-sac resorption as well as time mouth opening were recorded. Cardiac contractions per minute were also recorded at each measurement. One day before hatching, the flow (40-60%) was opened through 125- μ m mesh outlet filter. Upon resorption of the yolk-sac and opening of the mouth, the larvae were fed on rotifers, *Brachionus plicatilis*, cultured in a thermostatic chamber at 26°C and 25-28 psu. On day 13 after fertilization, all larvae have died, so observations and measurements were ended.

RESULTS

Mature unfertilized eggs were pelagic and spherical with a homogeneous and unsegmented yolk containing several oil droplets. Eggs were equipped with long filamentous appendages. The filaments are gathered together in a tuft. Fertilized eggs ranged in diameter from 1.58 to 2.05 mm, with a mean ($\pm$ SD) of 1.75 ± 0.10 mm. Table I illustrates changes observed during embryonic development at mean temperature of 19.2°C. After fertilization, a narrow perivitelline space developed. The first cleavage occurred about 1 h 15 min after fertilization, the second after 2 h 23 min and the third after 2 h 56 min. After 5 h 00 min, the blastoderm was in advanced stages of cleavage indicating a "mulberry" stage, while gastrulation started 8 h 50 min after fertilization. Formation of the embryo began after 25 h 33 min and somatic segmentation after 27 h 45 min. Between 27 and 37 h, optic vesicles formed and somites differentiation completed. After 31 h 50 min, somites and melanophores were

clearly visible on the body. The heart was observed beating after 40 h, while movements of the embryo were observed about 50 h after fertilization. Pectoral fin was visible 103 h 46 min after fertilization. After 113 h 21 min, progressive development of interior organs was visible. Oil globules in yolk aggregated at the vegetal pole. Vitelline circulatory system was unbranched and looping.

Hatching started after 211 h 32 min, and after 213 h 54 min all eggs hatched. Newly hatched yolk-sac larvae measured 4.5 mm ($\pm$ SD = 0.15) total length in average (range 4.4-4.7 mm). The newly hatched yolk-sac larvae were transparent and floated at the surface with the yolk-sac uppermost and sometimes in a lateral position without significant movements, except for sporadic tail thrusts. The fin fold encompassed much of the body. The trunk was segmented into 40-43 myomeres. The body was narrow and elongated, gut was short and the anus was anteriorly situated, the mouth was open, and the yolk-sac ovoid. The position of the oil globules was on the dorsal side of the yolk-sac. The anus was situated close behind the posterior margin of the yolk-sac. The larval pigmentation pattern was characteristic. It consisted of peritoneal pigment, an array of head melanophores, a long mediolateral stripe with many elongated melanophores (between 9-13 melanophores), a single row of ventral post-anal melanophores divided into two parts by the marginal fin: a single row of dorsal irregularly spaced melanophores, and pigment cells in the urostyle region. During development new melanophores were added, but the characteristics rows and arrays were maintained. By day 0, there were 3-5 melanophores in the otocystic region and 2-4 in the head region. The pectoral fin was clearly visible. By the end of day 1, foregut and hindgut were visible and about one third of the yolk-sac has already been absorbed. The position of the oil globules (ranged in diameter from 0.1 to 0.2 mm) were now on the right side of the yolk-sac. By the beginning of day 2, the mouth was completely functional (it ranged from 0.35 to 0.45 mm in width), and the anus was opened at the end of day 2. Oil globules came to lie near the heart. The yolk was completely reabsorbed by day 3. On day 4, the passage of food along the digestive tract of the larvae was clearly visible. The eye was completely pigmented. The body and

Table II. - Changes in length and shape of *Atherina boyeri* larvae during the first six days from hatching at mean temperature 19.2°C. [Changements de longueur et de forme des larves d'*A. boyeri* pendant les six premiers jours après l'éclosion, à la température moyenne de 19,2°C.]

Days from hatching	Total length (mm)	Notochord length (mm)	Yolk-sac volume (mm ³)	Eye diameter (mm)	Distance from snout to anus (mm)
0	4.35 $\pm$ 0.079	4.05 $\pm$ 0.016	0.52 $\pm$ 0.026	0.40 $\pm$ 0.011	1.50 $\pm$ 0.012
1	4.53 $\pm$ 0.068	4.35 $\pm$ 0.039	0.41 $\pm$ 0.024	0.42 $\pm$ 0.012	1.51 $\pm$ 0.011
2	4.70 $\pm$ 0.095	4.45 $\pm$ 0.035	0.19 $\pm$ 0.010	0.46 $\pm$ 0.015	1.55 $\pm$ 0.018
3	5.20 $\pm$ 0.095	4.90 $\pm$ 0.025	-	0.51 $\pm$ 0.005	1.82 $\pm$ 0.015
4	5.55 $\pm$ 0.110	5.25 $\pm$ 0.025	-	0.52 $\pm$ 0.004	2.11 $\pm$ 0.020
5	6.20 $\pm$ 0.095	5.75 $\pm$ 0.019	-	0.56 $\pm$ 0.005	2.74 $\pm$ 0.015

Table III. - Comparison of data for eggs and yolk-sac larvae of *Atherina boyeri* and other atherinid species. [Comparaison des données pour les œufs et les larves d'*A. boyeri* et d'autres espèces d'Athérinidés.]

Species	References	Egg diameter (mm)	Yolk-sac larvae (mm)
<i>Atherina boyeri</i>	Gourret (1893)	1.0	-
	Vialli (1937, in Boscolo, 1970)	1.0	5.5
	Sparta (1942)	1.72-1.76	-
	Jorne-Safriel and Shaw (1966)	-	6.0
	Castel <i>et al.</i> (1977)	-	6.0
	Palmer and Cully (1983)	0.1-1.8	-
	Creech (1992)	0.08-2.08	5.8
	Daoulas <i>et al.</i> (1997)	1.5	5.6-6.0
	Present study	1.58-2.05	4.4-4.7
<i>Atherina hepsetus</i>	Lo Bianco (1888)	1.5	-
<i>Atherina boyeri pontica</i>	Raffaele (1890)	-	7-8
	Marion (1894)	2.5	7-8
	Breder and Rosen (1966)	2.0	-
	Dekhnik (1973)	1.5-1.6	6.5
	Meshkov (1937, in Markevich, 1977)	-	5
<i>Atherina boyeri caspia</i>	Abdurakhmanov (1962)	1.2-1.7	5.0-5.5

notochord were straight. The greatest body depth ranged from 0.10 mm to 0.45 mm. A number of branching melanophores arised on the crown region of the head (from 2-4 to 5-6) at the beginning of day 5 after hatching. Few (3-4) melanophores also occurred at the base of anus and along the gut (together with two patches of pigmentation). The gut was short, with the preanal length averaging one-third the body length from hatching through the time of flexion. Pectoral fins are unpigmented. The ratio of the pre-anal length to the total length changed from 0.35 in newly hatched yolk-sac larvae to 0.42 in larvae, which are 6-day old. The backward migration of the anus was observed. Table II shows changes in length and shape of yolk-sac larvae and larvae during the first six days after hatching.

DISCUSSION

A comparison of egg diameters and total lengths of newly hatched yolk-sac larvae in *A. boyeri* and some other atherinids is presented in table III. Egg diameter is not a valuable parameter for identification, but it seems that some higher values (> 2.0 mm) were more frequently observed for *A. hepsetus* and *A. mochon pontica*. Marion (1894) and Breder and Rosen (1966) observed egg diameter ranged 2.0-2.5 mm for *A. hepsetus* (Tab. III), while Kanidev (1961) observed 2.3 mm for *A. mochon pontica*. (Tab. III). Numerous oil globules are found in the yolk of most atheriniform species, aggregating at the vegetal pole and may coalesce into a single droplet that comes to lie near the heart (White *et al.*, 1983). Several oil globules were observed in the yolk of *A. boyeri* in this study, but we did not observe coalescing of globules into a single droplet.

Although absent in some genera (*Leuresthes*, *Atherion*, and *Bedotia*), chorionic filaments are found on the eggs of most species. There is only one filament on the eggs of some atherinid species but most species have more (White *et al.*, 1983). The filaments can be scattered over the surface of the egg, as in *Atherinops* and *Atherinopsis*, or gathered together in a tuft as in *Atherina* (White *et al.*, 1983), what is also observed in present study. It is still difficult to assess the phylogenetic significance of this variation in the size, number and placement of the chorionic filaments (White *et al.*, 1983).

Morphologically, the larvae of the atheriniform fishes are much less variable than the eggs (White *et al.*, 1983). The length of the newly hatched yolk-sac larvae of *A. boyeri* from this study is significantly lower (t-test, $p < 0.05$) than those reported by other authors (Tab. III). In general, it seems that observed minimum lengths of newly-hatched yolk-sac larvae of *A. hepsetus* are higher than those for *A. boyeri* (Tab. III). This information may assist in identifying yolk-sac larvae of atherinids; however, it should be of limited value since, during the first few hours after hatching, yolk-sac larvae grew very rapidly and the length changed very quickly. The measurements in most studies were done on preserved specimens, so preservation in formalin or alcohol must be taken into account when comparing lengths of yolk-sac larvae, since it causes shrinkage.

The pigmentation patterns among yolk-sac larvae and larvae of *A. boyeri* from this study and from Lake Trichonis (Daoulas *et al.*, 1997) are in agreement (for the possible comparable range from 5.8 mm to 6.3 mm) in general mean. The characteristics of Lake Trichonis yolk-sac larvae and larvae agree well with the description of *A. presbyter* yolk-sac larvae and larvae from the English Channel and the

North Sea (Russell, 1976; Bamber *et al.*, 1985). They also agree with the description of *A. mochon* yolk-sac larvae and larvae (= *A. boyeri*, according to Tortonese (1975)) from the Mediterranean Sea (Vialli, 1937). However, the larvae described as *A. boyeri* by Vialli (1937) exhibit a weakly developed single row of ventral post-anal melanophores that are interrupted by extensive gaps, whereas the Lake Trichonis larvae display a well-developed row of regularly spaced melanophores. The descriptions and drawings provided by Dekhnik (1973) for the larvae of *A. mochon pontica* (= *A. boyeri pontica*) from the Black Sea are not detailed enough to allow a satisfactory comparison. However, it seems that the melanistic patterns of these larvae are different from those in our study. Yolk-sac larvae and larvae from this study also differ from the larvae of the Caspian taxon that have been described by Koblitskaya (1981) as *A. boyeri caspia*. In this case, the most notable difference is that in the Caspian population, the complete absence of dorsal melanophores and both the mediolateral stripe and the ventral row of melanophores of post-hatched embryos consist of only 6-8 melanophores, while in this study they consist of 9-13 melanophores. Post hatched embryos in the Trichonis population have both mediolateral stripe and the ventral row consist of 12-15 smaller melanophores (Daoulas *et al.*, 1997). In all atheriniform larvae a single row of melanophores develops on the dorsal margin and this contrasts with the Beloniformes and Cyprinodontiformes, where no consistent larval pigmentation pattern is evident (White *et al.*, 1983). The most important morphometric change during larval development was the backward migration of the anus. Daoulas *et al.* (1997) observed the ratio of the pre-anal length to the notochord or standard length changed from 0.30 in newly hatched larvae to 0.45 in larvae at the stage of metamorphosis, while in this study such ratio changed from 0.35 (newly hatched yolk-sac larvae) to 0.42 (in larvae six-day old). The preanal length of almost all known atheriniform flexion larvae is short, being approximately one-third of body length (White *et al.*, 1983).

Comparisons of embryonic and larval morphologies could, in certain cases, elucidate phylogenetic relationships, and therefore contribute to taxonomical clarification (Cohen, 1985). Such comparisons should be based on larval characters that exhibit minimal flexibility to environmental cues. Meristic and morphometric characters and developmental patterns that are extremely plastic should be avoided. Among the characters studied, only the pigmentation patterns exhibited a considerable stability and thereby were valid for comparisons with other taxa.

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